ON THE NATURE OF EDESTUS AND RELATED GENERA, WITH DESCRIPTIONS OF ONE NEW GENUS AND THREE NEW SPECIES.

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1. DESCRIPTIONS OF THREE NEW SPECIES OF EDESTUS

EDESTUS CRENULATUS, new species.

The type and only known specimen of this species belongs to the U. S. National Museum (Cat. No. 6050), and was found in a collection of fossils purchased from Mr. G. Hambach, of St. Louis, Missouri. No record regarding the origin of the fossil accompanied it, but there can be no doubt that the specimen had been obtained from the Coal Measures not far from St. Louis, probably from some of the coal mines of western Illinois. No species of the genus is mentioned in Mr. Hambach's Preliminary Catalogue of the Fossils Occurring in Missouri.[a]

The specimen (pl. 12, fig. 1) is almost as complete as it was on the death of the animal, only the apices of some of the teeth and some of the denticles being broken off and missing. The species resembles most that known as *Edestus heinrichii*,[b] but numerous differences may be observed.

The total length of the fossil is 207 mm.; the greatest height is 58 mm.; but to the latter measurement should be added about 2 mm. for the missing apex of the second tooth, counting from the right. The height of the shaft alone is 46 mm., the greatest thickness, beneath the first tooth, 28 mm. As will be seen from fig. 1, pl. 12, the

[a] Geological Survey Missouri, Bull. No. 1, 1890, pp. 60–85.

[b] Doctor Eastman (Bull. Mus. Comp. Zool., vol. 39, 1902, p. 65) points out that Newberry's specific name *heinrichsii* was improperly formed. Inasmuch as Newberry expressly says that the species was named for Mr. Heinrich, we may assume that the form *heinrichsii* was a *lapsus calami*, and on that ground adopt the form *heinrichii*. Newberry himself used this form in 1879 (Geological Survey Indiana, p. 347), although later he used the original spelling.

tooth-bearing border is arched, while the opposite border is slightly concave in each direction from near the middle of the length. A transverse section (text fig. 1) taken between the first and second teeth, counting from the right, shows that the lower border is here broadly rounded, while a section (text fig. 2) across the hinder half of the fossil shows that there the lower border is acute. Beginning just in front of the first tooth a sharp and narrow groove runs along the midline of the specimen, widening at the front end, then contracting and running backward on the lower side (text fig. 1, 7) to near the middle of the length.

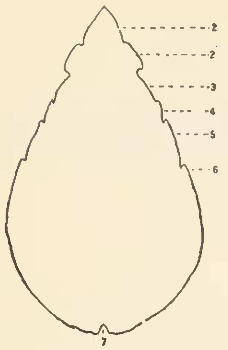

FIG. 1.—EDESTUS CRENULATUS, ×1. TYPE. VERTICAL SECTION BETWEEN THE FIRST AND SECOND TEETH. 2, SECOND SHEATH; 2[1], ENAMELED PROCESS OF SECOND TOOTH; 3, SHEATH OF THIRD TOOTH; 4, SHEATH OF FOURTH TOOTH; 5, SHEATH OF FIFTH TOOTH; 6, UPPER BORDER OF SHEATH OF SIXTH TOOTH; 7, GROOVE ALONG LOWER BORDER OF ANTERIOR HALF OF SHAFT.

Along the upper border of the fossil are six compressed teeth, the anterior and posterior borders of which are furnished with denticles. Of these denticles there are 8 or 9 on the anterior edge and perhaps 1 or 2 fewer on the hinder edge. Each of these denticles is minutely crenulated. Each tooth is covered by a layer of enamel, and at the base of the tooth a process of this enamel runs forward beneath the hinder third of the next tooth in advance. The following figures give the dimensions of the teeth. The length is taken from the point where the tooth joins the one in front to its contact with the next behind. The height is from the apex to the lower border of the enamel, along the axis. Tooth, 1; length of base, 26 mm.; height, 19± mm.: tooth, 2; length of base, 27 mm.; height, 19± mm.: tooth, 3; length of base, 27.5 mm.; height, 19 mm.: tooth, 4; length of base, 28 mm.; height, 19± mm.: tooth, 5; length of base, 30 mm.; height, 19± mm.: tooth, 6; length of base, 30.5 mm.; height, 18± mm.

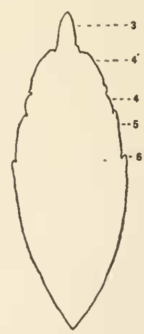

FIG. 2.—EDESTUS CRENULATUS, ×1. TYPE. VERTICAL SECTION BETWEEN THIRD AND FOURTH TEETH. 3, HINDER END OF THIRD TOOTH; 4, SHEATH OF FOURTH TOOTH; 4[1] ENAMELED PROCESS OF FOURTH TOOTH; 5, SHEATH OF FIFTH TOOTH; 6, UPPER BORDER OF SHEATH OF SIXTH TOOTH.

The thickness of most of the teeth at the lower end of the axis is 8 mm. The first one is slightly less; the last one is only 6 mm. thick. The angle between the anterior and posterior borders of any tooth is very close to 90°. It will be observed that the hinder tooth descends to the lower border of the shaft. The surfaces of all the teeth are smooth. A number of cracks in the enamel pass from the base of each tooth to the apex, and these seem to follow slight ridges.

The body of the fossil is made up of a shaft of vasodentine, dense and rough on the surface and without enamel. As has been shown by other observers, in the case of other species of the genus, this shaft consists of trough-shaped processes, one of which runs forward from each tooth, and which supports and partly incloses the process of the preceding tooth and is supported and partly inclosed by the succeeding one. The photograph (pl. 12, fig. 1) shows the grooves limiting each of these processes above and below. It will be seen that measuring each process, or sheath, from the hinder end of the tooth which it supports to its anterior end, the first one is 84 mm. long, the second 105 mm., the third 125 mm., the fourth 138 mm., the fifth 149 mm., the sixth 158 mm. This means that the anterior end of each sheath receded from the end of the shaft by considerably less than the length of the tooth to which it belonged.

This species appears to differ from *E. heinrichii* in various particulars, some of which will be mentioned.

1. The form of the shaft is different in the two species. In *E. crenulatus* the greatest height is in front of the middle of the length and under the second tooth; in *E. heinrichii* it is behind the middle and under the fourth tooth. It is possible that in the original of the figures of the last of these[a] the last-formed tooth is missing, but allowance for this would put the greatest height at the middle of the shaft. The shaft of *E. crenulatus* is relatively pointed in front; that of *E. heinrichii* is deep and truncated. If in the figured specimen of *E. heinrichii* the last-formed tooth is missing, a portion of its enamel ought to show under the last one present. If no tooth is missing, the shaft terminated in quite a different manner from that of *E. crenulatus*. Furthermore, in case the last-formed tooth of that specimen of *E. heinrichii* is missing there would have been present 9 teeth; in the type of *E. crenulatus* there are only 6. The type of *E. heinrichii* is a considerably larger specimen (280 mm. long) than that of *E. crenulatus*. It is difficult to see how the latter could become modified so as to resemble the former.

2. It will be noted the last sheath of *E. crenulatus* extends much farther forward than does that of *E. heinrichii;* also, it covers relatively less of the depth of the shaft.

3. In *E. crenulatus* a tongue-like process of the unenameled surface of the shaft runs backward between each tooth and the pointed process of enamel of the next tooth behind until it touches this hinder tooth; in *E. heinrichii* the tongue-like process is cut off from the hinder tooth by a prolongation of the anterior one.

4. The teeth of the two species are of different forms. In *E. crenulatus* the angle between the two lines carried from the apex of the

[a] Geol. Surv. Ill., vol. 4, pl. 1, fig. 1; Ann. N. Y. Acad. Sci., vol. 4, pl. 5, fig. 2.

tooth to the ends of the anterior and posterior cutting edges respectively is close to a right angle; in *E. heinrichii* the angle measures about 75°. The height of the teeth of *E. heinrichii* is six-tenths the length of the base, while in *E. crenulatus* it is seven-tenths. Nevertheless, the teeth of *E. heinrichii* appear more acute than those of *E. crenulatus* because of the concavity of the cutting borders, those of the latter species being nearly straight. The last tooth of *E. heinrichii* seems to be less elevated than the others. Judging from the apical angle and the straight cutting edges of the tooth, it is believed that Newberry's figure *2b* [a] represents a specimen of *E. crenulatus.*

It has been mentioned that there is in the specimen here described a narrow groove that runs forward from the first tooth, becoming broader at the end of the shaft. Immediately in front of this first tooth there is a rough surface just like that found bordering the enamel of each of the teeth. These facts suggest that some of the anterior and earliest formed teeth are now missing, that long before the animal died some teeth had dropped off. Certainly it is not probable that the animal became adult before it developed any teeth. There must have been a series of teeth from very small ones up to the first tooth now present. Nevertheless the writer does not believe that the shaft ever extended any considerable distance, if at all, in front of what is now its anterior end. No doubt the trough-like processes or sheaths of these earliest teeth, like those of the ones present, shortened rapidly toward the front, so that they probably never extended beyond the shaft as we now have it. Dr. Charles R. Eastman [b] has figured a series of three teeth which diminish rapidly in size, and in which the sheath of the smallest does not reach beyond the succeeding one.[c] Doubtless still smaller teeth occupied the space in front of the smallest one present. The significance then of the groove found in front of the first tooth of the type of *E. crenulatus* is found in the existence there, in the early youth of the animal, of a series of small teeth that were shed perhaps early in life.

Newberry [d] appears to have regarded the separate segment represented by his fig. *2a*, pl. 5, as that of a young animal. Its sheath is, however, too long for this. It must have been one of the later teeth. It seems possible that on sufficient maceration all the teeth, with their

[a] Ann. N. Y. Acad., vol. 4, pl. 5; Pal. Fishes N. A., pl. 39.

[b] Bull. Mus. Comp. Zool., vol. 39, p. 76, fig. 7.

[c] In case the reduction of Eastman's figure is really one-half, it seems possible that his specimen belongs to an undescribed species. Otherwise great variation in size of teeth in *E. heinrichii* is indicated. The length of the anterior teeth of the type is only about 30 mm., whereas the largest tooth figured by Eastman has a length of 37 mm.

[d] Ann. N. Y. Acad., vol. 4, p. 122.

sheaths, even of old individuals, might have separated from one another. The type of *E. karpinskii* lately described by Missuna[a] is evidently a segment produced by an adult individual and freed from all its predecessors.

At a short distance behind its anterior end each sheath of *E. crenulatus* is divided on the midline below into right and left portions, the lower edges of which run forward and upward. This is the origin of the groove which occupies the lower border of the front of the shaft. It is probable that in this groove at the point of separation of the lateral portions of the sheath the nerves and blood vessels entered and extended backward into each sheath and tooth.

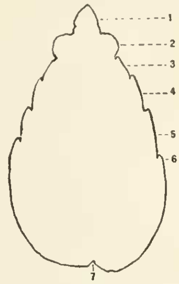

FIG. 3.—EDESTUS SERRATUS, ×1. TYPE. SECTION BETWEEN FIRST AND SECOND TEETH. 1, HINDER END OF FIRST TOOTH; 2, ENAMELED PROCESS OF SECOND TOOTH; 3, SHEATH OF THIRD TOOTH; 4, SHEATH OF FOURTH TOOTH; 5, SHEATH OF FIFTH TOOTH; 6, UPPER BORDER OF SHEATH OF SIXTH TOOTH; 7, GROOVE ALONG LOWER BORDER OF ANTERIOR HALF OF SHAFT.

It is, of course, possible that another tooth would have been produced behind the sixth of the type of *E. crenulatus;* but, in as much as that last tooth is considerably thinner than its predecessors, it is not unlikely that old age and decadence of powers had come on and that no more teeth would have been developed.

EDESTUS SERRATUS, new species.

The history of the type of this species is exactly that of the specimen described as *E. crenulatus*. It is Cat. No. 6049 in the U. S. National Museum. The length of the fossil (pl. 12, fig. 4), as found, is 150 mm. The sixth and last tooth of the series had been broken off before the time of entombment. If an allowance of 27 mm. is made for this missing part the whole length will be 177 mm. The greatest height, from the apex of the second tooth downward, is 51 mm. The greatest height of the shaft, between the second and third teeth, is 35 mm. Its greatest thickness is 21 mm.; that at the rear of the fifth tooth is 9 mm. The form of the shaft and sections of it (text figs. 3, 4) resemble those of *E. crenulatus*, but the hinder section, though not so high as that of *E. crenulatus*, is fully as broad. The last sheath occupies two-thirds of the width of the shaft. The anterior half of the shaft is rough, with close-set patches of enamel, irregular in size and form. The hinder half also is rough for some distance below the teeth, but most of the surface is nearly smooth. It seems possible that the hinder part of the shaft had been embraced by a sheath that had not

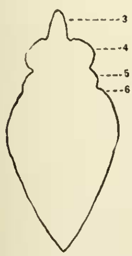

FIG. 4.—EDESTUS SERRATUS, ×1. TYPE. SECTION BETWEEN THIRD AND FOURTH TEETH. 3, HINDER END OF THIRD TOOTH; 4, ENAMELED PROCESS OF FOURTH TOOTH; 5, SHEATH OF FIFTH TOOTH; 6, UPPER BORDER OF SHEATH OF SIXTH TOOTH.

[a] Bull. Soc. Imp. Nat. Moscow, vol. 21, 1908, p. 528.

become consolidated, and which was lost when the specimen became interred. The point in the lower border from which the two concavities depart is directly opposite the space between the second and third teeth. In *E. crenulatus* it is opposite the apex of the second tooth.

The following are the dimensions of the teeth of this specimen: Tooth, 1; length of base, 22 mm.; thickness, 8 mm.: tooth, 2; length of base, 24 mm.; height, 19 mm.; thickness, 8 mm.: tooth, 3; length of base. 25 mm.; height, 19 mm.; thickness, 8 mm.: tooth, 4; length of base, 26 mm.; height, 19 mm.; thickness, 8 mm.: tooth, 5; length of base, 27 mm.; height, 19 mm.; thickness, 8 mm.

The apical angle of the teeth is 80°. That of *E. minor* is 35° or 40°; that of *E. crenulatus*, as already mentioned, is 90°. The anterior edge of the teeth is concave; the posterior is nearly straight. The teeth are furnished with denticles, but the edges of these are perfectly smooth. The surfaces of the teeth are enameled. From the base of each tooth a number of sharply defined and frequently anastomosing ridges rise to the apex. The forwardly directed process of each tooth is brought up close to the base of the next tooth in front.

In front of the first tooth there is, as in *E. crenulatus*, a groove that was originally occupied by a series of earlier-formed teeth. The higher and more pointed teeth, with concave anterior cutting edge and smooth denticles, distinguish this species from *E. crenulatus*, which it most resembles.

EDESTUS MINUSCULUS, new species.

Edestus cf. *minor* KARPINSKY, Verhandl. russ.-kais. min. Gesellsch. St. Petersb., 2d ser., vol. 26, 1898, p. 379, pl. 4, figs. 12, 13.

As cited above, Karpinsky identified provisionally as *E. minor* and described with illustrations a single tooth of an *Edestus* which had been found in the lowermost Permian, the Artinskian stage, near Moscow, Russia. A comparison of Karpinsky's description and figures with the numerous good figures that have been published of *E. minor* Newberry has convinced the writer that the tooth in question belonged to a species quite distinct from *E. minor*.

The tooth in Karpinsky's possession was a small one, the height from the base of the enamel to the apex, measured along the axis of the tooth, being only 14 mm., plus 1 mm. or 1.5 mm. that had been broken from the apex. It was therefore only about half as large as the specimen figured by Newberry [a] and by Eastman.[b] We must

[a] Geol. Surv. Ill., vol. 4, pl. 1, fig. 2. "*E. vorax*."

[b] Mark Anniversary Volume, pl. 21, figs. 2, 3.

conclude, therefore, either that it belonged to a much smaller species, than *E. minor* or that it belonged among the teeth of a half-grown animal.

If now, from Eastman's beautiful figures, apparently the best yet published, one compares the basal length of each tooth with its height, it is found that the ratio of the base to the height is 0.83, 0.82, and 0.81 in the first, second, and fourth teeth, respectively, 0.91 in the third and sixth, 0.93 in the fifth, and 0.97 in the seventh. While there are some irregularities here, no encouragement is given to concluding that the ratio would rise in the earlier-formed teeth. Now, the ratio of the base to the height in the tooth described by Karpinsky is 1.18. This means that in *E. minor* the base is considerably shorter than the height, while in the Russian tooth the base is considerably greater than the height.

An examination of the figures of *E. minor* shows that the hinder border of each tooth meets the anterior border of the next at an acute angle. Karpinsky's figure shows that the hinder free border of the tooth was turned at a right angle with the hinder cutting edge, an arrangement that would have made the angle between successive teeth quite different from that in *E. minor*. A somewhat similar process is seen at the hinder end of the last tooth of *E. crenulatus* and even of *E. minor*, but to assume that the Russian tooth was the last of the series is to abandon the supposition that it was the tooth of a young animal. Attention may also be called to the fact that in Karpinsky's specimen the apex of the concavity of the anterior border is placed between the middle and lower thirds of the border, while in *E. minor* it is placed considerably lower down; also that the hinder cutting edge of *E. minusculus* is far more strongly convex than that of *E. minor*.

In the specimen studied by Karpinsky the height of the sheath, taken at the front end of the tooth, is 0.3 the basal length of the tooth. If the last tooth of *E. minor* had the same length as the one immediately in front of it, the height of the sheath, obtained at the hinder border of the last tooth present, would be 0.75 of the length of its tooth.

The section of the sheath of his specimen that Karpinsky has published requires notice.[a] This section shows that the lower border, close to the tooth, was rounded, not sharp, as it is in *E. crenulatus*, *E. serratus*, and *E. heinrichii*. No section of *E. minor* has hitherto, so far as the writer knows, been published. Prof. F. S. Loomis, of Amherst, Massachusetts, has kindly sent me an accurate drawing of the broken hinder end of the type of the species, now deposited in the

[a] Verhandl. russ.-kais. min. Gesellsch. St. Petersb., 2d ser., vol. 26, 1898, p. 380, fig. 16.

collection of Amherst College. This drawing, here reproduced (text fig. 6), represents a section across the sheath immediately in front of the eighth tooth, now missing. For comparison with it is shown Karpinsky's section of his specimen (text fig. 5). The difference will be readily observed. It may be noted here that Mr. E. T. Newton published [a] a description of a species of *Edestus*, *E. triserratus*, found in the coal measures of Britain. The shaft appears to have been much curved. Beneath the tooth the lower border is thin and angular. In front of the tooth the border is broadly rounded.

FIG. 5.—EDESTUS MINUSCULUS, ×3. TYPE. SECTION OF SHEATH JUST IN FRONT OF TOOTH.

2. ON THE HISTOLOGY OF EDESTUS.

The organ called *Edestus*, whatever its position and its function, is composed of dentine which is penetrated by numerous terminal arteries and veins and capillary canals. On the surface of what are called teeth is a thin layer of what is probably true enamel. The dentine must be classed with that called by Tomes vasodentine, although, like osteodentine, there existed no distinct pulp. Some sections have been made, in order to show the minute structure of the organ in question. These have been prepared from two specimens of what are regarded as *Edestus heinrichii*, which have been most kindly sent me by Dr. Bashford Dean, of the American Museum of Natural History, New York. The specimens came originally from western Indiana. There is represented in fig. 1, pl. 13, a section across one of the segments, so taken as to include the front of the tooth. That part which belongs to the tooth broke away from the part below it during mounting. An examination of this figure shows that in this genus the central core of dentine, which contains the larger vessels, was not sharply marked off from the more superficial portions, as it is marked off in *Helicoprion*, as shown by Karpinsky. Below the center of the section there is a large vessel that probably corresponds to Karpinsky's "Längscanal." The section appears to have fallen where the canal was sending off a large branch. In the specimen figured all the larger vessels and many of the smaller ones apparently have the lumen open. They are really filled with a transparent mineral, probably calcite. Each, however, has a narrow black border which represents a deposit of pyrite or marcasite. Many of the capillary channels appear to be filled with pyrite, but this appearance seems often to be due to the position of the vessel in the section, for when the near and the distal walls

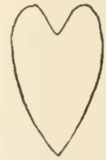

FIG. 6.—EDESTUS MINOR, ×1. TYPE. SECTION OF SHEATH JUST IN FRONT OF TOOTH.

[a] Quart. Jour. Geol., vol. 60, 1904, pp. 1–8, pl. 1.

have been cut away the lumen appears. As the surfaces of the organ are approached, the filling of the channels with pyrite becomes more complete. In fig. 1 of pl. 13 and also in fig. 2, in order to bring out the structure, the lumina of the vessels are represented as black. The light spaces between the network of black lines represent the dentine substance.

Examination of the section shows that the longitudinal canals, large and small, are abundantly connected by anastomosis, so that the vascular apparatus formed a dense network. In the lower portion of the section, that corresponding to the root of the tooth, many of the larger capillary canals approach the surface, and probably some of them passed out into the surrounding tissues. Fig. 2 on pl. 13 represents a median sagittal section of another small segment of *Edestus*. This is taken in front of the tooth and includes no part of it. Most of the vascular canals run longitudinally. The main longitudinal canal is seen near the bottom of the section. As seen in favorable situations, fine branching lines run away from the borders of the capillary canals. These lines are regarded as marking the dentinal tubes. Often, especially near the capillaries (pl. 13, fig. 3, taken from near the anterior border of a tooth), they have the lumen filled with pyrite, and then they resemble the canaliculæ of bone. Where not indicated by pyrite filling, the tubes may nevertheless often be traced out under the microscope, and they constitute a network of fine lines in the dentine. Nowhere does there appear to be any layer of dentine made up of tubes running parallel with one another.

The layer of enamel is so deeply stained with pyrite that few observations can be made on it. In one spot it is sufficiently thin and translucent to allow it to be seen that the enamel is penetrated by nearly parallel black lines, which stand at right angles with the outer surface of the tooth, but do not quite reach this surface. This is to be taken as that variety of enamel described by Tomes as being penetrated by dentinal tubes.[a]

Karpinsky[b] has noted the resemblances between the teeth of *Helicoprion* and those of various sharks, living and extinct. The present writer has wished to compare *Edestus* with the spines of fossil sharks, and has accordingly made sections of a fragment of the spine of *Ctenacanthus varians* (pl. 13, figs. 4, 5). Although differences between this genus and *Edestus* may be observed, the writer regards the structure of the two as being essentially the same. In the specimen of *Ctenacanthus* nearly all the capillary vessels are probably filled with limonite, while few of the dentinal tubes are thus filled.

[a] Manual Dental Anat., 6th ed., p. 30.

[b] Verhandl, russ.-kais. min. Gesellsch. St. Petersb., 2d ser., vol. 26, 1898, p. 420.

The larger blood vessels do not appear to be so richly connected by capillaries as in *Edestus*. Under high power a dense network of bright lines, which are regarded as representing the dentinal tubes, is to be seen, running irregular courses and branching dichotomously. The shadowed areas seen around most of the capillaries are produced by the network of dentinal tubes, slightly stained with iron.

3. DESCRIPTION OF NEW SPECIMENS OF LISSOPRION FERRIERI.

In 1907 [a] the writer described a fossil which he regarded as related to *Edestus*, but still more closely to *Helicoprion*. The type specimen, now the property of the U. S. National Museum, Cat. No. 6091, had been found in Upper Pennsylvanian deposits, near Montpelier, Bear Lake County, Idaho, by Mr. W. F. Ferrier. At the time of publishing the description it was impossible to determine whether the complete structure would prove to be straight or slightly bent, as the species of *Edestus*, or strongly bent, as the fossil described by Dean as *Edestus lecontei*, or spirally coiled, as *Helicoprion bessonowi* Karpinsky. Immediately after the appearance of that description the writer received from Mr. Ferrier two shipments of specimens from the same horizon at Thomas Fork, Wyoming, not far from the type locality. These showed that the series of teeth and their shaft formed a spiral resembling closely that of *Helicoprion*. From the best of these specimens have been prepared figs. 1 and 2, on pl. 14. At a later time, about October 1, 1907, Mr. Ferrier made a fourth shipment, consisting of a block of limestone, in which there was a complete example of this curious fossil (pl. 15). Unfortunately the limestone is excessively hard and tough, while the fossil teeth and their shaft are friable. As a result the plane of cleavage has passed through the shaft and most of the teeth instead of over their surfaces. Nevertheless the specimen displays well the coils of the spiral and the outlines of most of the teeth. Taking all the specimens together, the most important facts regarding the structure are made known. Credit is due Mr. Ferrier for his interest in collecting so much material belonging to this species. He has, moreover, presented to the U. S. National Museum the type of the species and important parts of the other specimens. Mr. Ferrier is a geologist and paleontologist of much experience, having been for some years assistant to Sir William Dawson, of the Geological Survey of Canada, and being now engaged as mining engineer in charge of phosphate mining for a commercial company.

Besides the specimens of *Lissoprion* Mr. Ferrier has collected many invertebrate fossils from the deposits that furnished *Lissoprion*, and

[a] Science, vol. 26, p. 22.

these fossils are being described by Dr. George H. Girty, of the U. S. Geological Survey. Doctor Girty has very kindly furnished me some information regarding these fossils and their relationships. He writes me that the specimens of *Lissoprion* were obtained from phosphate beds of from 60 to 100 feet in thickness and placed near the middle of the Preuss formation. The fauna has a facies strongly unlike anything known from the Pennsylvanian of eastern North America, and many features tend to ally it with the upper Carboniferous faunas of eastern Europe and Asia. In fact Doctor Girty feels little doubt that it is equivalent to a part of the Gschel stage of the Russian section. Some of the characteristic fossils of the phosphate fauna are *Chonetes ostiolatus*, *Pugnax weeksi*, *Ambocœlia arcuata*, *Nucula montpelierensis*, *Yoldia mcchesneyana*, *Leda obesa*, *Plagioglypta canna*, *Omphalotrochus ferrieri*, *O. conoideus*, and *Gastrioceras simulator*. The genus *Productus* is poorly represented in the phosphate fauna, but contains four species closely related and perhaps identical with forms occurring in the Gschelian of Europe. These species, with the species of *Omphalotrochus* and others occurring in the overlying strata of the same formation, are the forms in which the affinities with the Russian fauna are especially manifested.

In the case of the specimen which furnished fig. 1, pl. 14, the rock split in such a way as to expose the right-hand side of the first five large teeth, those at the termination of the shaft, and the left side of the fifth of these (counting from the end), two others succeeding this, and several small teeth of an interior whorl, as well as a part of the shaft. The figure has been prepared by combining two photographs, that of the left side having been reversed. The designation of the sides as right and left is made on the assumption that the base of the spiral, the larger end, was directed backward in the animal, a view that may require modification. The 5 or 6 teeth seen in the lower part of fig. 1, pl. 13, formed probably the beginning of the second whorl, no remains existing in the specimen of the first or innermost whorl. Some traces are found in the matrix of the remainder of the second whorl. The large teeth would then belong to the third whorl.

It will be observed that the shaft of the specimen extends backward (toward the left) some distance beyond the last tooth produced, and the same will be found to be true of the species called by Dean *Edestus lecontei*. The last tooth present can hardly have been the last one that would have been developed had the animal lived longer, for this tooth lacks much of having the size of the teeth of the type specimen. In this the largest tooth has a height of 36 mm. and a width of 17 mm., while the last tooth of fig. 1, pl. 14, has an axial height of 30 mm. and a width of 11 mm.

The small teeth of fig. 1, pl. 14, present only a part of their upper portion, or blade.

The specimen represented by fig. 2, pl. 14, presents wholes or parts of 13 teeth and the corresponding part of the shaft. Plate 15 is taken from the specimen that displays the whole of the spiral. Unfortunately the matrix is of such a dark color that the fossil does not show as distinctly as is desirable. However, from this it is learned that the structure, dentition or spine, whichever it may be, consisted of a shaft of a little more than two and a half coils and a series of enameled teeth occupying the outer border of the shaft. The inner coil with its minute teeth was, of course, first produced. It is not probable that the smallest teeth seen are the first that the animal possessed. Some smaller teeth and their shaft may be hidden in the obdurate matrix, but it is more probable that they had been lost by the animal long before its death.

The greatest diameter of the specimen, measuring from the apex of the last tooth to the apex of the one on the opposite side of the coil is 160 mm. The inner coils were not in contact with the outer coil nor with each other. The apices of the teeth at the beginning of the second coil are removed by about 10 mm. from the inner border of the shaft; the innermost teeth approach within 3 mm. of the shaft. It is impossible to determine exactly the whole number of teeth. An estimate made as accurately as possible indicates that there were 32 teeth in the outer coil, the same number in the preceding coil, and 22 teeth in the portion remaining of the innermost coil, in all 86 teeth, as against 130 in *Helicoprion bessonowi;* but the latter species possessed about one more coil than did the species here described. In Karpinsky's species there were 36 teeth in the innermost coil, 43 in the next, and 51 in the outer.

Karpinsky showed that the teeth of his species might be regarded as consisting of three portions. The first includes the cutting blade, extending from the apex to the points where the edges of the blade come into contact with the blades of the succeeding and the preceding teeth, respectively; the third portion includes that part that is narrowed and turned toward the older teeth of the series; the second portion is found between these two. In the larger teeth of *Helicoprion* the intermediate portion occupies half or more of the height of the tooth; in the case of the smaller teeth it becomes reduced in importance and may become merged into the third portion. In *Lissoprion* this middle part may be said to be present in all the teeth, but to be relatively unimportant. In *Helicoprion* the blade is relatively longest in the oldest, or smallest, teeth, forming sometimes more than half the height of the tooth, while in the largest teeth it forms only about a fourth of the height. In all cases the blade forms, in *Lissoprion*, about one-half the total height of the tooth.

The apical angle of the teeth before us is obtained by drawing lines from the apex to the opposite ends of the cutting edges. This angle varies with the size of the teeth. In the teeth originally described, the largest yet found, the apical angle is 48°. In the largest teeth of pl. 14, fig. 1, the angle is 35°, while in the teeth of the specimen represented by pl. 14, fig. 2, it is 32°. The smallest teeth appear to have the same angle as just given. It is seen, therefore, that the angle increases rapidly in the largest teeth. Karpinsky has stated [a] that in *Helicoprion bessonowi* the apical angle is 30°. The present writer makes it 45°.

The cutting edges of the teeth of *Lissoprion* were originally described as being smooth; but some of the newer specimens show that these edges were sometimes feebly crenulated.

The middle portion of each tooth is short, convex posteriorly, concave anteriorly. It passes insensibly into the third portion. The latter is narrowed to a point below and turned toward the older parts of the coil. In the smaller and medium-sized teeth its extremity reaches forward to a point opposite the hinder border of the second tooth in advance. In the larger teeth it extends forward only to the middle of the tooth immediately in front. Each tooth touches its predecessor and its successor only at the base of the blade. The median and third portions of the successive teeth are separated by a space very narrow and varying little in relative width throughout the series. In *Helicoprion bessonowi* the interdental spaces vary considerably, being much wider relatively between the smaller teeth.[b] All the teeth of *Lissoprion* were covered with enamel, but this has, in the specimens at hand, been altered or removed. It seems to have been traversed by narrow ridges, which radiated from the apex of the tooth.

Fig. 2, of pl. 14, furnishes a good illustration of the shaft and its relation to the teeth. It will be observed that a wide band of the shaft is exposed below the enameled processes of the teeth, the width in the case of the specimen figured being 6 mm., one-fifth the height of the teeth and the shaft taken together. In *Helicoprion* there is far less of the shaft visible below the teeth; according to Karpinsky's figures, about one-fifteenth of the height of the teeth and the shaft. Text fig. 7 shows a section through the axis of the second tooth from the right. It is seen that the sides of the shaft are convex and that in the lower border there is a rounded notch. This represents a gutter that runs along the inner border of the shaft. A similar gutter occu-

[a] Verhandl. russ.-kais. min. Gesellsch. St. Petersb., 2d ser., vol. 26, 1898, pp. 383, 402, fig. 23.

[b] Idem, p. 394, figs. 24–29.

pies this border in *Helicoprion;* and Karpinsky thinks that it might have conducted some kind of vessel. According to his view, the gutter was completed below by a layer of shagreen, but I find no evidences of any such a covering. The sides of the shaft are unbroken and the edges bounding the gutter are smooth.

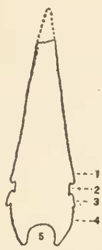

FIG. 7.—LISSOPRION FERRIERI, ×1. SECTION OF SHAFT AND TOOTH. 1, ENAMEL OF THIRD TOOTH; 2, GROOVE BETWEEN NARROWED PROCESSES OF THIRD AND SECOND TEETH; 3, ENAMELED PROCESS OF SECOND TOOTH; 4, EXPOSED PORTION OF SHAFT; 5, GROOVE ALONG LOWER BORDER OF SHAFT.

The lateral surfaces of the shaft are covered by a layer which looks as if it might be enamel. For some distance below the teeth this is pitted so as to resemble in miniature the pittings of the carapace of a trionychid turtle; but low down the enamel is raised into delicate ridges that run parallel with the shaft. Doctor Eastman has, in defining *Helicoprion*, stated that the sides of the shaft are traversed by a double lateral groove. This is, however, an error, which has doubtless arisen from a slight misconception of the sections published by Karpinsky.[a] In those figures the two notches on each side represent, not sections of as many longitudinal grooves, but of grooves between the downward prolongations of the crowns of the teeth. There are no longitudinal grooves in *Lissoprion* and no room for them on the sides of the shaft of *Helicoprion.*

4. DESCRIPTION OF A NEW GENUS.

TOXOPRION, new genus.

The type of this genus is Dean's *Edestus lecontei.* Doctor Eastman has recognized that this species did not belong to *Edestus*, inasmuch as he included it in his genus *Campyloprion;* and afterwards, on removing the type of the genus, *C. annectens* to *Heliocoprion*, he essayed to make *lecontei* the type. The writer called attention to this matter in 1907.[b] Even were this procedure admissible it would not be advisable, for the species *annectens* may yet prove to belong to a genus distinct from *Helicoprion* and would then require the name *Campyloprion.*

The teeth of *Toxoprion* resembled most those of *Lissoprion*, but the shaft, though strongly bent, formed only a part of one coil. In this genus the present writer includes H. Woodward's *Edestus davisii*, found in Australia. In this species it will be observed that the width is considerably reduced in passing from the newer to the older ends of the specimen, so that it is not likely that a complete coil was

[a] Verhandl. russ.-kais. min. Gesellsch. St. Petersb., 2d ser., vol. 26, 1898, p. 397, figs. 30, 31.

[b] Science, vol. 26, p. 22.

formed. It will be seen, too, that the teeth change considerably as they are followed from one end of the shaft to the other. In the newer ones the downward prolongations are pointed and carried forward even to the extended axis of the fourth tooth in advance, while in the smaller and older teeth the prolongations are truncated and reach only the extended axis of the second tooth in advance. The part of the shaft exposed is very narrow.

5. DEFINITIONS OF THE GENERA.

It is evident that *Lissoprion* is closely related to *Helicoprion*, but it is believed to be sufficiently distinct. It is possible that future discoveries may abolish the differences noted.

Edestus.—Shaft straight or slightly bent, roots of the teeth betraying distinct traces of their original distinctness, and forming the greater portion of the fossil. Blades of the teeth strongly denticulated. Type, *E. vorax* Leidy.

Toxoprion.—Shaft bent, but forming less than a complete coil, mostly concealed under the bases of the teeth. Roots of teeth showing no traces of their original distinctness in the shaft. Blades of teeth high, pointed, feebly denticulated. Type, *T. lecontei* (Dean).

Lissoprion.—Teeth and their shaft forming a spiral, the coils not in contact. Roots of teeth indistinguishably consolidated. Shaft widely exposed below the teeth. Inner border of shaft with a longitudinal groove. Teeth high, the middle portion short, the cutting edges smooth or feebly denticulated. Type, *L. ferrieri* Hay.

Helicoprion.—Teeth and shaft forming a spiral, the coils not in contact. No traces of the separate roots of the teeth. Blades of teeth distinctly denticulated. Little of the shaft exposed below the bases of the teeth. A longitudinal groove along inner border, as in *Lissoprion*. Middle portion of teeth variable; in the larger teeth greatly developed. Type, *H. bessonowi* Karpinsky.

6. THE NATURE OF THE OBJECTS CALLED EDESTUS, TOXOPRION, LISSOPRION, AND HELICOPRION.

In discussing this subject it is not necessary to enter into the history of opinions regarding the position occupied and the function performed by the structures that have been described above. The literature of the subject may be found cited in Doctor Eastman's papers.[a] In the first of these papers this author, who has devoted so much attention to the fossil fishes and with such profit to science, discusses the homology of the objects before us. He there frames a strong argument in favor of regarding them as the consolidated symphysial teeth of the lower jaws of sharks. Karpinsky had pre-

[a] Bull. Mus. Comp. Zool., vol. 39, pp. 55–99, and in the Mark Anniversary Volume, pp. 281–289.

viously expressed the opinion that the spiral of *Helicoprion* was composed of the symphysial teeth of the upper jaw, the spiral having been pushed outside of the mouth and carried above the snout.

Eastman based his conclusions on the fossil called *Campodus*, which he shows was composed of the symphysial teeth of probably the lower jaw. This row of teeth would correspond to the median row of lower teeth in *Heterodontus philippi*, the Port Jackson shark. If in this shark the outer and older teeth should, instead of dropping off, cohere with the younger teeth, there would be formed at least two-thirds of a coil, a structure that would resemble that of *Campodus*. If, then, the teeth should become strongly compressed the mass would resemble considerably that object that we call here *Toxoprion*. Further coiling would result in a series like *Lissoprion*.

However, when we come to homologizing *Edestus*, *Lissoprion*, and *Helicoprion* with the teeth of *Campodus* and *Heterodontus* difficulties are encountered. In the case of the two latter genera, the difficulty is to determine what disposition to make of such large spirals. If in *Heterodontus* the symphysial teeth should cohere with one another, a spiral of several coils might eventually be formed; but unless there were some especial arrangement developed, the spiral could be completed only by a pushing of the older end of it through the skin and into the flesh and cartilage of the jaw. This would not contribute to the comfort of the animal or the strength of the jaw, however much it might aid our efforts at homologizing. It would be necessary, too, to conjecture a shark with a lower jaw of tremendous proportions to accommodate a spiral like that of *Helicoprion*, the diameter of which is sometimes as much as 260 mm. If it be said that the spiral projected far enough beyond the jaw to escape burial in the tissues, it may be objected that it would have been in a position to be troublesome to the animal and exposed to injuries. The slender and bent dental mass of *Toxoprion*, too, would have hung down in a position dangerous to its existence.

A strong objection to placing any of these fossils in the mouth of a shark is to be found in the fact that none of them show any indications of wear. The species of *Edestus*, described above, present no attrition of the enamel or of the most delicate denticles or crenations. Dr. A. S. Woodward, in speaking of *Helicoprion* [a] has sought to escape this objection by supposing that the rows of teeth were so far apart that they did not rub against one another. Nevertheless, constant contact with the food taken into the mouth must have produced some wear.

It seems certain that the general conclusions of Karpinsky regarding *Edestus* and *Helicoprion* must be accepted, namely: (1) These

[a] Geol. Magazine, dec. 4, 1900, vol. 7, p. 33.

animals belonged among the Elasmobranchii; (2) the organs that represent to us these sharks were more or less imbedded in the soft parts; (3) they must have been organs in the median plane of the body; (4) a considerable part of each of these organs must have been exposed externally—that is, they were not wholly buried in the flesh. If these supposed dental masses were in the mouth they were consolidated teeth. The blades and the processes of enamel descending from them correspond to the crown of the teeth, while the shaft was formed through more or less complete fusion of the roots of the teeth. Now, while the crowns of the teeth in *Edestus* resemble closely those of some kinds of sharks, it must not be supposed that the cutting edges and the denticles correspond to those of sharks. Through strong compression of the teeth the original cutting edges would have been brought to occupy what is now the middle of the lateral faces of the teeth, while the anterior and posterior midlines would have become the cutting edges. The denticles of these edges were developed later and could not have been derived from the original denticles. It will be seen, therefore, that the whole tooth, if a tooth, suffered great transformation.

If the organs under consideration were not teeth they must have been placed either in front of some of the median fins, like many of the other ichthyodorulites, or possibly behind a dorsal fin, like the stings of the Masticura, or on the back of the head, as the spine of *Xenacanthus*. As regards *Edestus*, it does not seem to be important whether the new segment of the compound spine, if spine it was, came up before or behind the older ones, since probably the whole shaft was buried in the flesh. If it came up behind the older ones the spine might have been directed horizontally from the fin; if the new tooth arose in front of the older ones the spine may have been directed upward and backward in the fleshy front of the fin. If in the case of *Helicoprion* and *Lissoprion* the new tooth had arisen behind the older ones the spiral would have been directed forward, and on being subjected to oblique blows would have been liable to be twisted from its socket. It seems almost certain, therefore, that the new teeth came up in front of the older ones, in case, of course, the organ belonged outside of the mouth. If this is true, the end that has in this paper been called the front end is the hinder end and the end called the hinder is the front end.

The stings of the Masticura appear to be shed and replaced by new ones. In *Aëtobatis* there may be as many as five or six of these spines present at once. The statements regarding the origin of the new spines do not agree. Günther[a] says that in the Trigonidæ the stings are shed from time to time and replaced by others growing

[a] Study of Fishes, p. 342.

behind the one in function. Newberry[a] states that the worn spine is succeeded by another from behind. Jækel[b] writes that usually one finds in front of the base of an old spine the germ of a new one. In a specimen of *Rhinoptera bonasus* in the U. S. National Museum there is found a very small spine, loosely attached, in front of the one in function. In the German edition of Günther's Study of Fishes, translated by Hayek (p. 236), is a figure of the tail of a *Myliobatis* bearing two spines, the smaller of which is in front of the larger one. Storer,[c] speaking of *Myliobatis acuta*, states that the smaller spine is in front of the larger. It appears, therefore, that in the Myliobatidæ the new spine comes up in front of the older ones. On the other hand, Mr. B. A. Bean, of the U. S. National Museum, has shown me a specimen of *Urolophus jamaicensis* and one of an undetermined species of *Tæniura* in which a considerably smaller spine is behind the functional one; from which fact it may probably be inferred that in the Dasyatidæ the new spine arises behind the one in function.

It appears to the writer, therefore, that the objects called *Edestus*, *Lissoprion*, *Helicoprion*, etc., may for the present be most easily disposed of by supposing that some ancient elasmobranchs developed in front of a median dorsal fin, or in place of it, not a single spine, but a succession of them. The new compressed spine, serrated in front and behind, arose in front of the older ones. Nevertheless, the root of the new spine became directed backward beneath and on each side of the preceding one, so as partly to embrace it. At first probably the older spines were shed, but in time they began to cohere and thus form a compound spine. In *Edestus* this was straight or slightly bent. All of it, or nearly all, except the serrated teeth, was buried in the flesh. As more and more elements were added, the organ became more curved and finally in some species formed a spiral, which was directed backward and the last turn of the shaft of which was elevated enough to keep the teeth from cutting into the skin. Such a weapon could be brought into action if only its possessor had dived under its victim and brought the spine across its abdomen, thus disemboweling it, a suggestion already made by Trautschold. It is in this way, as Doctor Gill informs me, that *Gasterosteus* attacks its enemies.

If possibly these organs belonged in front of a dorsal fin, that of *Edestus* might have had its shaft buried in the fleshy part of the front of the fin and directed upward and backward. The spiral of *Helicoprion* may be supposed to have been coiled on one side of the fin to which it belonged. The fin would have formed a partial sheath for the spiral.

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[a] Paleoz. Fishes N. A., p. 224.

[b] Sitz.-Ber. Naturfor. Freunde, Berlin, 1890, p. 124.

[c] Fishes of Massachusetts, p. 270.

EXPLANATION OF PLATES.

Plate 12.

Figs. 1–3. *Edestus crenulatus*, $\times\frac{4}{5}$.

Fig. 1. View of right side.

2. View of section at the fracture through the second tooth from the right.

3. View of section at the fracture through the fourth tooth from right.

4. *Edestus serratus*, $\times\frac{4}{5}$. View of right side.

In Figs. 2, 3, the narrow white lines are at the boundaries between the contiguous sheaths.

Plate 13.

Figs. 1, 2. *Edestus heinrichii*, $\times 6$.

Fig. 1. Cross-section through shaft and front of tooth.

2. Vertical sagittal section of shaft and part of tooth.

In both of the figures the vascular channels are represented in black.

3. *Edestus heinrichii*, $\times 45$.

Part of sagittal section through tooth to show vascular canals and the dentinal canals diverging from them.

4, 5. *Ctenacanthus varians*, $\times 6$. Cat. No. 6048, U.S.N.M.

4. Transverse section. The vascular canals are black.

5. Longitudinal section.

Plate 14.

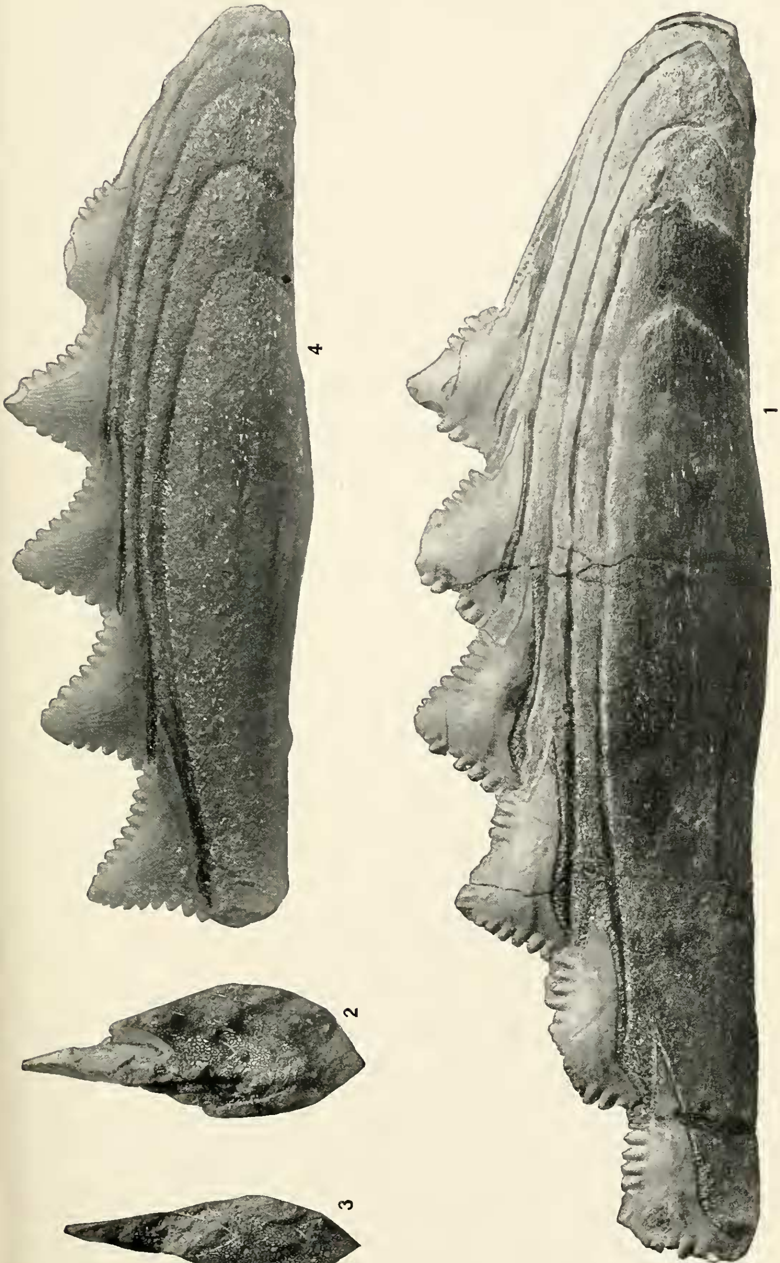
Lissoprion ferrieri, $\times\frac{9}{10}$.

Fig. 1. Part of the outer whorl, with 7 large teeth, and some small teeth of an inner whorl.

2. The axis and about 12 teeth of another specimen.

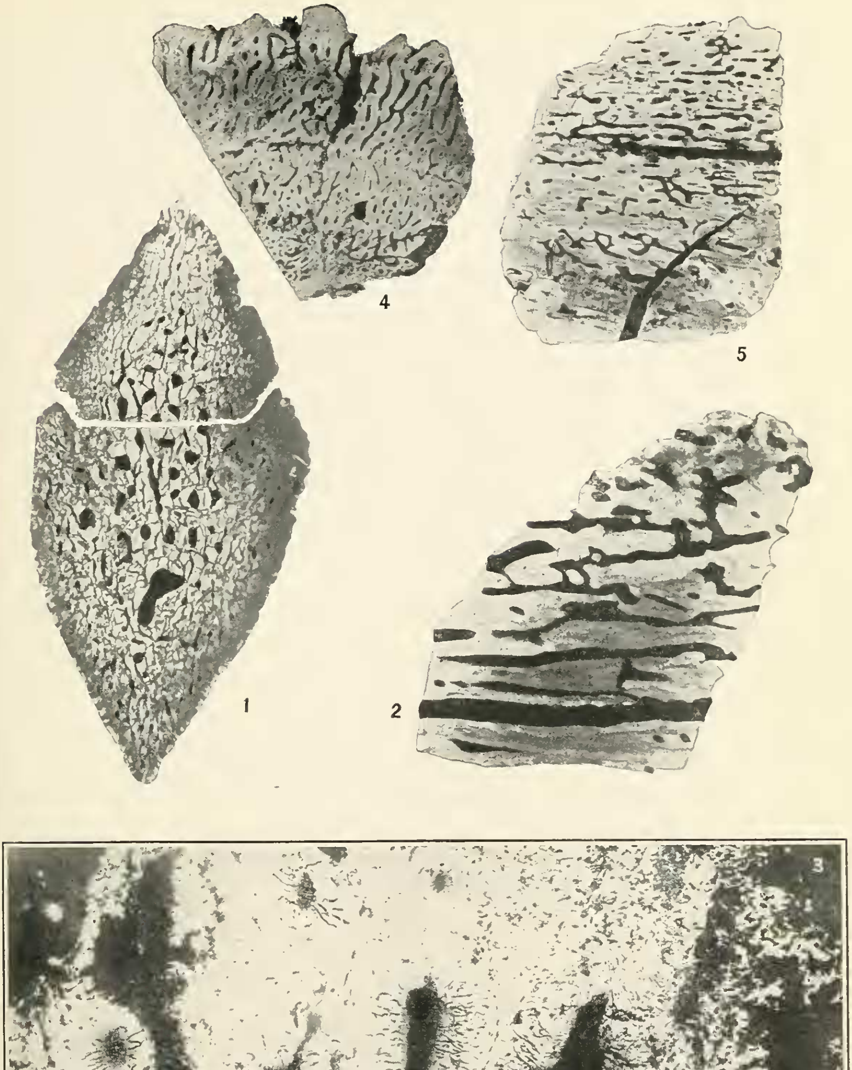
Plate 15.

Lissoprion ferrieri, $\times\frac{9}{10}$. View of spiral showing the whorls and some of the teeth.



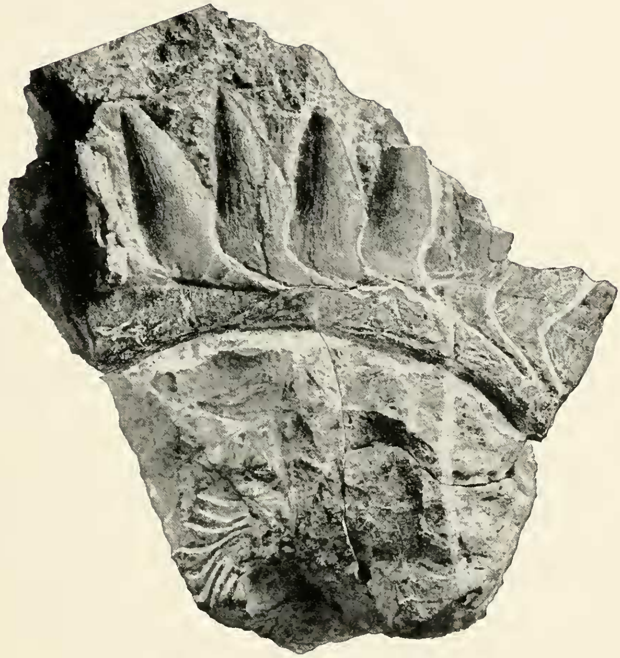
EDESTUS CRENULATUS AND EDESTUS SERRATUS.

FOR EXPLANATION OF PLATE SEE PAGE 61.



EDESTUS HEINRICHII AND CTENACANTHUS VARIANS.

For explanation of plate see page 61.



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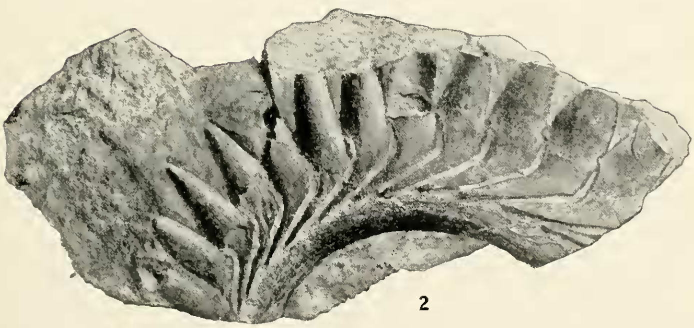

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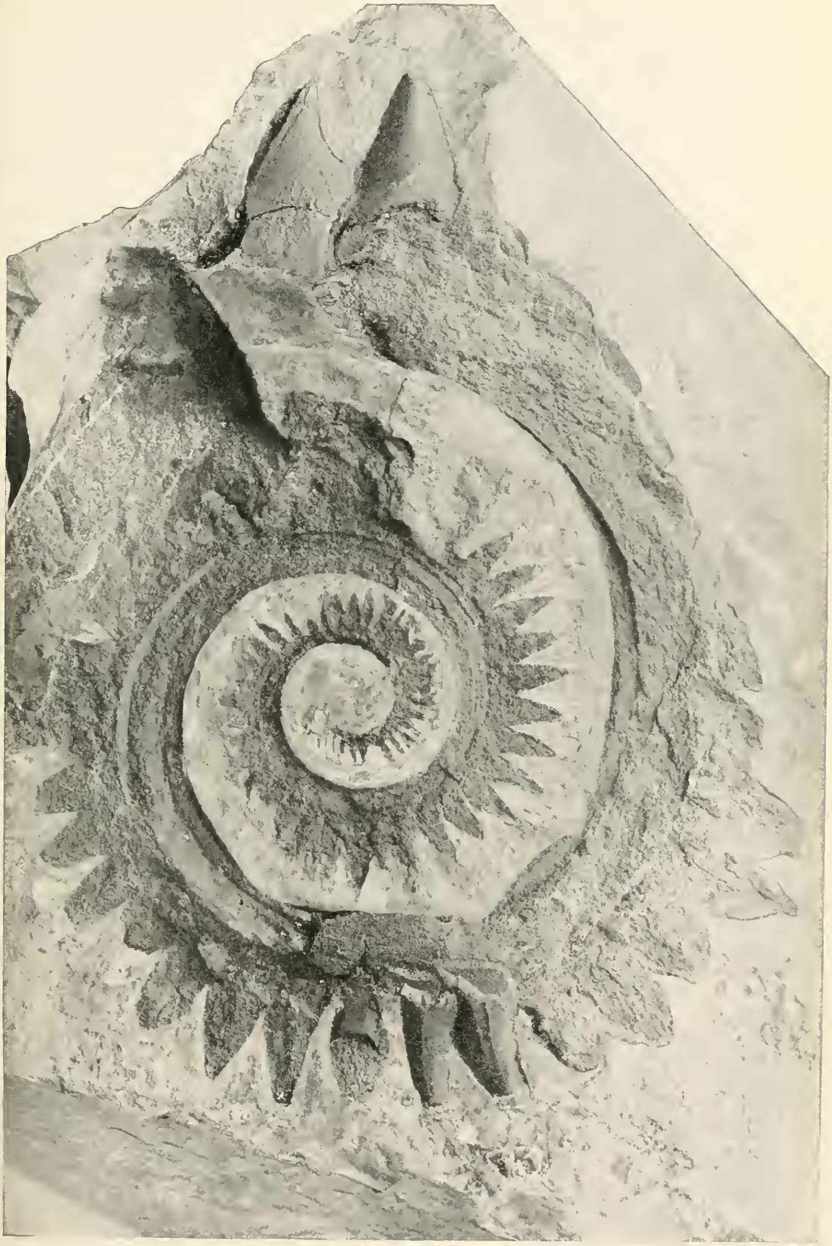
LISSOPRION FERRIERI.

FOR EXPLANATION OF PLATE SEE PAGE 61.



LISSOPRION FERRIERI.

FOR EXPLANATION OF PLATE SEE PAGE 61.